

The University of Chicago

INFLUENCE OF POTASSIUM
AND SODIUM ON METABOLISM OF
PEANUT COTYLEDONS DURING
GERMINATION

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF BOTANY
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By
HUBERT J. DYER

Reprinted from
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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 585

HUBERT J. DYER

Introduction

It had been noticed that, when cocklebur was grown under potassium-deficient conditions, the cotyledons persisted in a fleshy and turgid condition much longer than did those of control plants. It was conjectured that this persistence might be a result of impedance of the vascular

transport of food reserves from the cotyledons, since both breakdown (15) and interference with formation of phloem tissue (26) have been described as potassium-deficiency symptoms.

An experiment was designed to investigate the relative rates of removal of the important cotyledonary food reserves

under conditions of adequate (+K) versus no (-K) potassium supply, as well as to study other symptoms associated in the -K syndrome. Since seeds of cocklebur were unavailable in large quantities, Virginia peanut seed was chosen as the test object. It has the advantages of being large, fatty, and epigeal in germinating habit. The experiments were carried out in the dark to avoid confusion of the interpretation by the addition of new products of photosynthesis.

operations were carried out by the light of a 15-watt blue bulb shielded except at the tip and carried in the hand. The plants were grown for 6 (experiment I) or 7 (experiments II and III) and for 15 days (all experiments).

At harvest the sand was washed from the root systems. It was found impossible, however, either to retain all the brittle lateral roots of the 15-day plants or to remove the sand from the roots completely by washing and rinsing with concentrated sodium chloride solution. There-

TABLE 1
COMPOSITION OF NUTRIENT SOLUTIONS USED

Salts (Stock solutions)	Solution A (+K-Na)	Solution B (-K+Na)	Solution C (-K-Na)
Ca(NO ₃) ₂ 0.05M	20 ml./l.	20 ml./l.	20 ml./l.
MgSO ₄ 0.05M	10 ml./l.	10 ml./l.	10 ml./l.
KH ₂ PO ₄ 0.05M	10 ml./l.		
NaH ₂ PO ₄ 0.05M		10 ml./l.	
Ca(H ₂ PO ₄) ₂			(0.0025M)
H ₃ BO ₃ 0.0463M			
MnCl ₄ 0.0064M			
ZnSO ₄ 0.00076M	1 ml./l.	1 ml./l.	1 ml./l.
CuSO ₄ 0.0003M			
H ₂ MoO ₄ 0.0004M			
Fe ₂ (C ₄ H ₄ O ₆) ₃ 0.0089M	1 ml./l.	1 ml./l.	1 ml./l.
Atmospheres	1.12	1.12	1.05

Material and methods

In each experiment Virginia peanuts obtained from a commercial seedsman were shelled, examined, and selected for undamaged seeds. They were planted in washed quartz sand in glazed pots, the drains of which were covered with glass wool. Each pot was watered before and after planting and thereafter daily or every second day, depending on the experiment, with its appropriate nutrient solution. Nutrient solutions (table 1) were based on those suggested by HOAGLAND and ARNON (9). The pots were kept in a basement room of relatively even temperature, and the room was maintained in complete darkness except at times of watering and harvest. These

fore, the root systems of the 15-day plants were severed from the hypocotyls at the point of divergence of the first lateral root and were discarded.

Immediately at harvest the wet weights of the 6- or 7-day cotyledons and axes (hypocotyl plus epicotyl) and of the 15-day cotyledons, hypocotyls, and epicotyls were taken separately. The axial tissues were dried in an air-blast oven at 150° C. for 5 minutes; then the temperature was reduced to 70° C. to complete the drying. After drying for 4 hours, they were placed in desiccators and held until weighed. The fresh cotyledons from each treatment were harvested in triplicate lots, weighed in pairs, and the lot members mixed together. Each lot was ground

in a meat-chopper with 2 gm. of calcium carbonate for each 100 gm. of tissue in such a manner that the discharge from the mill dropped into boiling redistilled ethanol in quart mason jars. The jars were sealed and held in a dark cabinet until the contents could be analyzed.

Methods for chemical analyses were those described by LOOMIS and SHULL (13), except that lipids were determined by the method of SANDO (20) and lipolytic activity was estimated by the method of LONGENECKER and HALEY (12) on fresh cotyledons. Invert sugars and crude fiber were both determined by difference (total sugar — reducing sugars = invert sugars; total dry matter — dry weight of determined substances = crude fiber). Comparisons of wet-weight and dry-weight data were made by the analysis of variance technique described by SNEDECOR (23).

Material for histological study was killed in CROOKS's modification of Navashin's solution (3), washed in tap water for 48 hours, dehydrated in a tertiary butanol-ethanol series, imbedded in paraffin, sectioned at 15 μ , and stained with Flemming's triple stain.

DESCRIPTION OF EXPERIMENTS

In experiment I, selected peanut seeds were further selected by rejecting all seeds falling outside the limits of ± 0.05 gm. of the mean seed weight. The seeds were planted as described above, and either solution A or solution B (table 1) was applied daily. Three lots of each treatment were harvested at 6 days after planting and three more lots at 15 days. Analyses were made for lipids on the absolute basis only.

Experiment II was performed similarly to experiment I, except that the first harvest was taken on the 7th rather than on the 6th day after planting. Anal-

yses were made of these samples of cotyledons for moisture, total sugars, reducing sugars, starch and dextrins, acid-hydrolyzable substances, soluble nitrogen, insoluble nitrogen, and total lipids.

Experiment III was designed similarly to experiments I and II, with the following exceptions: three instead of two nutrient solutions were used: A, B, and C (table 1); pots were treated with nutrient solution every second day; and the seeds, instead of being merely selected for size, as in experiments I and II, were, in addition, individually weighed and their weights recorded. Solution C was designed to furnish the same amount of H_2PO_4^- ions as solutions A and B, to supply neither potassium nor sodium, to cause as small a difference as possible from the other two solutions in the concentration of calcium, and to have approximately the same ionic concentration as the other solutions. Plants were again harvested at 7 and at 15 days after planting. In this experiment wet weights of the 7-day cotyledons and axes and of the 15-day cotyledons, hypocotyls, and epicotyls were taken; dry weights of 7-day axes and of 15-day hypocotyls and epicotyls were also recorded. Dry weights of cotyledons could not be obtained because of the analytical procedure used.

Results

Removal of the two predominant complex reserve materials, fats and proteins, from the cotyledons proceeded somewhat slowly for the first 6 or 7 days after planting but went on much more rapidly during the next 8 days (fig. 1). It is assumed from the data (tables 2-4) and from the fact that cotyledons of etiolated seedlings were not visibly necrotic until 4 weeks after planting that the quantity of lipid and protein reserves remaining in peanut cotyledons during germination

and early growth follows an inverse sigmoid curve with time the abscissa. The effect of substitution of sodium for potassium in the nutrient substrate appears to be to flatten this curve; this is most marked at the 7-day point. Wider differences are evident between treatments in dry weight of cotyledons, dry weight of entire plants, and grams of lipid and protein per 100 plants at the mid-point of the experimental period than at the end. The 7-day plants had less dry matter both in axes and in cotyledons, and less

lipid and protein in the cotyledons under $-K +Na$ conditions (solution B) than under $+K -Na$ (solution A). Although carbohydrates in the cotyledons, especially starch, increased somewhat during germination, the increase was not in the same ratio in experiments II and III, nor was it consistent with treatment. There was a reversal between the 7th and 15th day in the distribution of lipids between treatments in all three experiments: whereas more lipid remained in the $+K -Na$ cotyledons at 7 days, by the

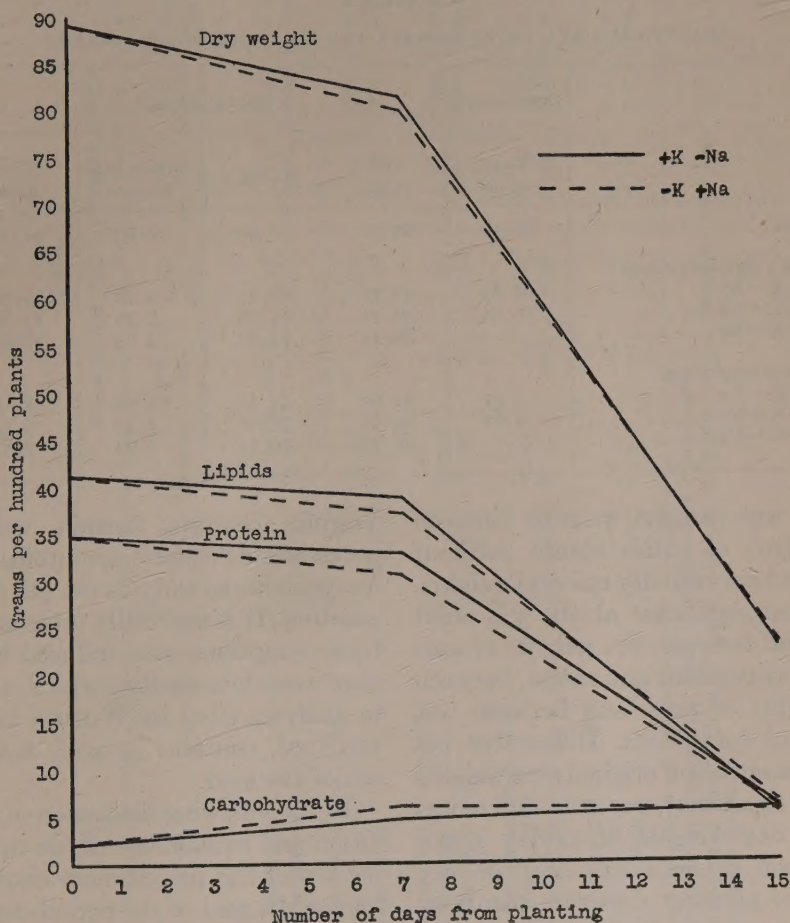


FIG. 1.—Changes in amount of dry weight, carbohydrates, lipids, and proteins in cotyledons of Virginia peanuts during first 15 days after planting in dark as affected by substitution of sodium for potassium (data of experiment II).

15th day they had lost more lipid than the $-K + Na$ cotyledons. When both potassium and sodium were eliminated from the nutrient solution (solution C, experiment III), lipids were not so rapidly lost as when either was present, and the amounts of starch found in the cotyledons more nearly approximated those for the $+K - Na$ treatment.

Statistical analysis of the wet- and dry-weight data for 15-day plants from experiment III (table 4) revealed highly significant differences owing to treatment

treatments. Histological study of the vascular tissue of the cotyledonary petiole revealed no evidence of breakdown and no differences between treatments in amount of phloem present. Tests of lipolytic activity performed *in vitro* on fresh cotyledons using peanut oil as a substrate showed no differences in fat-hydrolyzing rate between treatments.

Discussion

When potassium was lacking from the nutrient medium during germination of

TABLE 2
ANALYTICAL DATA, EXPERIMENTS I AND III, GRAMS PER 100 PLANTS

	EXPERIMENT I	EXPERIMENT III			
	Total lipids	Dry weight	Moisture	Starch and dextrins	Total lipids
Seeds.....	36.31	89.01	18.52	0.92	41.26
6- or 7-day cotyledons:					
+K-Na.....	18.87	76.37	68.27	4.72	26.96
-K+Na.....	17.78	70.72	77.06	3.59	22.26
-K-Na.....		74.77	73.83	4.63	27.58
15-day cotyledons:					
+K-Na.....	3.83	35.90	55.37	2.70	6.18
-K+Na.....	4.62	37.05	58.63	2.42	6.33
-K-Na.....		36.79	60.34	2.93	7.33

between wet epicotyl weights, between wet weights of entire plants (without roots), and between dry epicotyl weights. Differences significant at the 5% point were found between wet weights of axes (without cotyledons and roots), between dry weights of axes, and between wet weights of cotyledons. Differences between treatments of original seed weights were not significant, nor were differences between dry weights of 15-day hypocotyls, nor between any wet or dry weights of parts or complete plants at 7 days.

There was no visible difference among the roots of plants from the various

Virginia peanuts, certain well-known potassium-deficiency symptoms became recognizable as early as the 7th day after planting. It is especially interesting that these symptoms were induced in such a short time in a seedling which, according to analyses cited by WINTON and WINTON (27), contains 35-40% K_2O in the ash of the seed.

In the following discussion of the condition and metabolism of the cotyledons the writer has placed more emphasis on the middle part of the period covered by the experiments (although not to the exclusion of the later conditions); it is thought that their metabolism during

TABLE 3
ANALYTICAL DATA, EXPERIMENT II

	Dry weight	Moisture	Reducing sub- stances	Invert sugars*	Starch and dex- trins	Acid- hydro- lyzables	Soluble nitrogen	Insoluble nitrogen	Total protein	Total lipid	Total carbo- hy- drate	Crude fiber†
Seed:												
% of dry weight.....	17.22‡		0.02	1.15	1.10	None	0.06	6.28	39.26	48.95	2.27	9.46
Gr./100 plants.....	18.52		.02	0.97	0.92	None	0.05	5.59	34.94	41.26	1.91	8.42
7-day cotyledons (+K - Na):												
% of dry weight.....	50.16‡		.08	1.70	4.01	None	0.05	6.44	40.23	47.19	5.79	6.74
Gr./100 plants.....	82.33		.06	1.40	3.28	None	0.04	5.26	32.90	38.00	4.74	5.51
7-day cotyledons (-K + Na):												
% of dry weight.....	51.23‡		.10	1.82	5.38	None	0.05	6.17	38.55	46.41	7.30	7.69
Gr./100 plants.....	83.99		.09	1.53	4.30	None	0.04	4.93	30.83	37.12	5.92	6.15
15-day cotyledons (+K - Na):												
% of dry weight.....	78.33‡		.40	4.20	19.65	0.39	1.12	4.02	25.10	22.06	24.73	26.99
Gr./100 plants.....	82.50		.09	0.98	4.48	0.09	0.26	0.92	5.73	5.03	5.64	6.16
15-day cotyledons (-K + Na):												
% of dry weight.....	76.50‡		.23	3.67	18.02	0.33	0.96	4.02	24.79	27.16	22.25	24.84
Gr./100 plants.....	75.20		0.05	0.85	4.16	0.07	0.22	0.93	5.81	6.27	5.13	5.74

* Determined by difference: total sugars - reducing sugars = invert sugars.

† Determined by difference: total dry matter - total dry weight of determined substances = crude fiber.

‡ Per cent of total weight.

TABLE 4
WET AND DRY WEIGHT DATA, EXPERIMENT III

Material	Treatment	Mean weight (gm.)	Standard deviation	F	Degrees of freedom
7-day plants:*					
Original seeds, air-dry.....	{ +K-Na	0.869	0.072	1.315	2, 105
	{ -K+Na	0.860	.067		
	{ -K-Na	0.889	.086		
Cotyledon pairs, wet.....	{ +K-Na	1.431	.133	1.376	2, 105
	{ -K+Na	1.444	.128		
	{ -K-Na	1.469	.137		
Axes plus cotyledons, wet.....	{ +K-Na	3.006	.279	1.151	2, 105
	{ -K+Na	2.928	.260		
	{ -K-Na	2.986	.230		
Axes alone, wet.....	{ +K-Na	1.551	.251	1.076	2, 105
	{ -K+Na	1.472	.220		
	{ -K-Na	1.509	.211		
Axes alone, air-dry.....	{ +K-Na	0.160	.098	2.329	2, 105
	{ -K+Na	0.146	.024		
	{ -K-Na	0.152	.026		
15-day plants:†					
Original seeds, air-dry.....	{ +K-Na	0.858	.092	2.105	2, 97
	{ -K+Na	0.898	.104		
	{ -K-Na	0.858	.075		
Cotyledon pairs, wet.....	{ +K-Na	0.849	.183	4.509‡	2, 97
	{ -K+Na	0.941	.216		
	{ -K-Na	0.991	.164		
Axes (without roots) plus cotyledons, wet.....	{ +K-Na	5.615	.796	7.066§	2, 97
	{ -K+Na	5.292	.772		
	{ -K-Na	4.906	.578		
Axes without roots or cotyledons, wet.....	{ +K-Na	4.721	.671	4.760‡	2, 97
	{ -K+Na	4.374	.853		
	{ -K-Na	4.067	.929		
Axes without roots or cotyledons, air-dry.....	{ +K-Na	0.422	.066	4.692‡	2, 73
	{ -K+Na	0.401	.052		
	{ -K-Na	0.369	.067		
Epicotyls, wet.....	{ +K-Na	2.402	.428	10.899§	2, 97
	{ -K+Na	2.139	.388		
	{ -K-Na	1.872	.370		
Epicotyls, air-dry.....	{ +K-Na	0.229	.046	6.325§	2, 93
	{ -K+Na	0.215	.034		
	{ -K-Na	0.195	.032		
Hypocotyls, without roots, air-dry.....	{ +K-Na	0.186	.039	1.933	2, 77
	{ -K+Na	0.187	.034		
	{ -K-Na	0.176	0.044		

* Based on thirty-six plants in each treatment.

† Based on twenty-three to thirty-five plants in each treatment.

‡ Significant at odds of 19:1.

§ Significant at odds of 99:1.

this earlier period was more free than during the later period from the effects of the hunger metabolism which supervenes as the cotyledonary reserves become exhausted and which might be expected to mask the effects of the treatments (22).

DRY MATTER.—Dry weights of cotyledons and plant axes at 7 days were less under $-K -Na$ and much less under $-K +Na$ conditions than in the controls (tables 2-4). This is interpreted as confirming the frequently reported symptom of potassium deficiency—exalted respiratory rate (7, 19, 25). In addition, it indicates that the presence of large amounts of available sodium in the absence of much potassium induces a higher respiratory rate than is shown by plants deprived of both sodium and potassium. Such a situation has not come to the writer's attention through the literature. This differential in loss of dry weight between treatments is paralleled by a differential in rates of utilization of lipid and protein reserves.

Dry weights of cotyledons at 15 days were least under $+K -Na$ and greatest under $-K +Na$ conditions; this apparently is analogous to the situation earlier observed in cocklebur. At the same time, weights of plant axes and entire plants were greatest under $+K -Na$ and least under $-K -Na$ conditions. It is thought that this change in relationships compared with the status at 7 days was due to the change in character of growth between the 7th and 15th days; during this period the entire lateral root system of the seedling was developed. At the 7th day the primary root was short, smooth, and branchless, while at the 15th day its upper half was covered with laterals varying in length from 3 to 4 cm. at the base of the hypocotyl to mere swellings at the mid-length of the primary root. The development of so many

additional terminal meristems would impose a seriously accelerated demand on the potassium reserves of the seed (5, 15, 21); it could thus bring on not only the reversal of relative respiratory rates between the two treatments but the stunting of the epicotyls of the $-K -Na$ plants in comparison with the other two ($+K -Na$ and $-K +Na$) treatments. In the $-K +Na$ plants the situation is not so severe, probably because of the effectiveness of sodium in partially relieving the potassium deficiency (1, 8, 11).

Moisture contents of cotyledons (tables 2, 3), of axes, and of entire plants at 7 days were slightly higher in $-K +Na$ than in other treatments. Differences in moisture content between treatments at 15 days were not consistent in experiments II and III. In general, the moisture content differences were small and afforded little basis for conclusions with respect to the effect of potassium deficiency on turgidity of tissues.

CARBOHYDRATES.—Carbohydrates are of minor importance from a quantitative standpoint among the peanut seed reserves, as they constituted only 2.27% of the dry weight of the cotyledons. Data for carbohydrates in the cotyledons also show conflict between experiments II and III; this may have been because of slight differences in experimental conditions between experiments. Such differences would be accompanied by small differences in metabolic states of the developing tissues which might have been great enough to cause the conflicting results.

In experiment II the amount of carbohydrate in the cotyledons was inversely related to the amount of lipid remaining; this is what would usually be expected from a consideration of the results of PETERS (16), LASKOVSKI (10), MILLER

(14), and others with germinating fatty seeds. This was not confirmed, however, by experiment III.

In contrast to the observation of DAY (4), but in agreement with that of NIGHTINGALE *et al.* (15) on tomato stems, there was no apparent interference with the plant's ability to form starch in these experiments under $-K + Na$ nutrient conditions, since appreciably more starch was found in the cotyledons at 7 days (experiment II) and in the histological sections of $-K + Na$ petioles and hypocotyls at both 7 and 15 days than in the $+K - Na$ plants.

PROTEIN.—The fate of the protein reserves was similar to that of the other complex reserves. The cotyledons behaved like the senescent leaves described by RICHARDS and TEMPLEMAN (19) in that proteolysis proceeded rapidly, thus making the amino acids available to the growing axis. The rate of protein loss from the cotyledons was increased by $-K + Na$ conditions compared with the control (fig. 1, table 3) during the earlier period of growth; eventually the values for protein remaining in the cotyledons under the two treatments drew together again as the reserve protein approached exhaustion at the 15th day. This situation is similar to those described by RICHARDS (17) and by WALL (25), in which high respiratory rate and $-K + Na$ nutrition were combined; in this case, however, they were not accompanied by more soluble nitrogen, at least in the cotyledons, probably because all available soluble nitrogen compounds were being used in protein synthesis in the rapidly growing axis. This would be expected, especially if potassium is necessary specifically for the early stages of nitrate reduction (15) or for the conversion of ammonium to other soluble nitrogen compounds (18), but not if po-

tassium is necessary only for the final stages of protein synthesis from amino acids (7, 25). In this regard the writer follows the opinion expressed by TIEDJENS and WALL (24) in discussing the effect of potassium deficiency on carbohydrate formation—that these effects are “due to injury to the protoplasm because ion balance is lacking rather than to any specific unfilled catalytic role of potassium.” In other words, the imbalance resulting from the substitution of potassium by sodium or any other ion disturbs protoplasmic function along a wide front, which seems plainly evident from the results of these experiments.

LIPIDS.—The curve representing the rate of loss of lipids from the cotyledons (fig. 1) parallels that for the decrease in amount of protein present, except that the rate was slightly faster over the 15-day period. In the case of lipids, as with proteins, $-K + Na$ conditions led to more rapid loss of reserves during the earlier part of the period studied than was true under $+K - Na$ conditions. This may have been merely a response to the greater respiratory rate of the $-K + Na$ plants. It is thought, however, that such an explanation fails to account for the larger amount of carbohydrates in the $-K + Na$ plants. It seems that there may be a direct effect of $-K + Na$ nutrition to increase the lipolytic rate in the cotyledons. A hypothesis might be advanced that potassium plays a specific role in protecting the lipid reserves from the lipolytic enzymes and that, when sodium is substituted for potassium, either (a) the permeability to the enzymes of the membrane surrounding the lipid droplets is lowered, or (b) the surface per gram of lipid is so greatly increased owing to the lowering of the interfacial tension between the fats and the protoplasm that much more rapid destruction

of the fats by lipase results, or (c) both. Modification of the permeability of membranes surrounding an enzymatic substrate has been suggested by COVILLE (2) to account for the change of starch from a state of immunity to one of vulnerability toward diastase, or the reverse, in the continuous presence of that enzyme.

The reasoning in regard to the relationship of sodium and potassium to the protection of the lipid substrate from esterases is supported by the work of CLOWES and of HARKINS and ZOLLMAN as described by GORTNER (6). These workers showed that sodium chloride in solution greatly increased the surface of a given quantity of olive or paraffin oil dropped into the solution by lowering the interfacial tension of the system, while calcium chloride exerted the opposite effect. It will be noted that the $-K -Na$ plants, which were grown with a slight excess of calcium in comparison with the other two treatments, retained more lipid in the cotyledons than either of the other two groups of plants both at 7 and at 15 days after planting.

Lipolysis may be so rapid under certain circumstances (experiment II) that carbohydrates originating from the breakdown are "forced" into a storage state by mass action; or, on the other hand, it may proceed somewhat more slowly (experiment III) or may be exceeded by an exalted respiratory rate to such an extent that appreciable storage carbohydrates do not result. It is thought that this is a pertinent consideration in attempting to explain the failure of experiment III to duplicate the trends in carbohydrate distribution shown by experiment II.

In explaining the occurrence of more lipid in the $-K +Na$ cotyledons at 15

days than in the $+K -Na$ cotyledons (the reverse of the situation at 7 days), two suggestions may be made. One is that prolonged potassium starvation resulted in malfunctioning of the translocating mechanism specifically with respect to the products of lipid destruction and that this depressed the hydrolysis of storage fats toward the end of the experimental period. There was evidence of the accumulation of carbohydrates in the cotyledons of the $-K -Na$ plants of experiment III, which might possibly be considered as owing to interference with their translocation. Such an explanation would not only be contrary to the conclusions of NIGHTINGALE *et al.* (15), who found translocation unimpeded under $-K$ conditions, but would also be at variance with the facts that (a) no anatomical differences in phloem structure between treatments was evident and that (b) there was no interference with amino acid translocation. Invocation of any such explanation would thus imply a translocation mechanism of great specificity, in which the transport of one class of substances normally transported could be impeded independently of other classes of substances. On the other hand, slight reduction of the cross-sectional area of phloem tissue has been reported by WATTS (26) to accompany potassium deficiency in the seedling tomato, and it does not seem impossible that a certain amount of impedance or malfunctioning of the translocation tissue could exist before it becomes evident microscopically.

The preferable explanation seems to be that the reversal of rate of utilization of lipid reserves between treatments was bound up in a manner unknown at present with the radical change in morphology and physiology of the developing seedling which intervened between the

7th and 15th days (see above, "Dry matter").

Summary

1. Virginia peanuts were grown in the dark in pots of quartz sand and were watered daily or every second day with either a complete nutrient solution (+K -Na), a solution in which sodium had been substituted for potassium (-K +Na), or one in which neither sodium nor potassium was present (-K -Na).

2. Cotyledons were harvested at the 6th or 7th and again at the 15th day after planting, were counted, weighed, and analyzed for reducing and total sugars, starch and dextrins, acid-hydrolyzable substances, soluble and insoluble nitrogen, and total lipids.

3. At 7 days carbohydrates were more abundant and lipids and crude protein less abundant in the -K +Na than in the +K -Na cotyledons. At 15 days the lipid relationship had reversed itself. Plants grown with -K -Na solution had somewhat more lipid material in their cotyledons at each stage than either of the other groups.

4. Determinations of lipolytic activity and histological study of the vascular structure of the cotyledonary petiole revealed no differences between treatments at 7 or 15 days.

5. The total dry weight of plants at both 7 and 15 days was less for -K +Na than for +K -Na plants; this is interpreted as indicating a higher

respiratory rate owing to potassium deficiency.

6. The more rapid utilization of protein under -K +Na conditions is probably a reaction to the low availability of potassium for the catalysis of nitrate reduction. Since the latter condition limits the opportunity for the formation of amino acids in the -K plants, such new protein as is formed in the developing seedling axis must come from resynthesis of the proteins withdrawn from the reserve areas.

7. Histological preparations revealed the presence of several times as much starch in the seedling axis of the -K plants as in the controls. This appears to be confirmatory of the seedling's inability to utilize carbohydrate in protein synthesis.

8. No definite evidence of interference with translocation under -K conditions was found.

9. It is suggested that potassium may have a specific role in protecting the lipid substrate from lipase.

10. Additional evidence was obtained that sodium may to a certain extent alleviate potassium deficiency.

Sincere appreciation is expressed for the advice and encouragement of Professors SCOTT V. EATON and CHARLES A. SHULL, as well as other members of the Department of Botany of the University of Chicago who assisted the writer in many ways during the course of this work.

LITERATURE CITED

1. BLANCK, E. Die Bedeutung des Natriums für die Pflanze und die sogenannte Kochsalzdüngung. *Fühlings Landw. Ztg.* 65:441-463, 508-535. 1916.
2. COVILLE, F. V. The influence of cold in stimulating the growth of plants. *Jour. Agr. Res.* 20: 151-160. 1920.
3. CROOKS, D. M. Histological and regenerative studies on the flax seedling. *BOT. GAZ.* 95:209-239. 1933.
4. DAY, DOROTHY. Starch formation in tobacco plants deficient in potassium. *Plant Physiol.* 15:367-375. 1940.
5. DICKSON, J. G. The value of certain nutritive elements in the development of the oats plant. *Amer. Jour. Bot.* 5:301-325. 1918.

6. GORTNER, R. A. Outlines of biochemistry. 2d ed. Wiley & Sons, New York. 1938.
7. GREGORY, F. G., and SEN, P. K. Physiological studies in plant nutrition. VI. The relation of respiration rate to the carbohydrate and nitrogen metabolism of the barley leaf as determined by nitrogen and potassium deficiency. *Ann. Bot.* 1:521-561. 1937.
8. HARTWELL, B. L., and PEMBER, F. R. Sodium as a partial substitute for potassium. *Rhode Island Agr. Expt. Sta. Ann. Rept.* 21:243-285. 1908.
9. HOAGLAND, D. R., and ARNON, D. I. The water-culture method for growing plants without soil. *Calif. Agr. Expt. Sta. Circ.* 347. 1938.
10. LASKOVSKI, N. Ueber eine chemische Vorgänge bei der Keimung der Kürbissamen. *Landw. Vers. Sta.* 17:219-244. 1874.
11. LEHR, J. J. The importance of sodium for plant nutrition. *Soil Sci.* 52:237-244. 1941.
12. LONGENECKER, H. E., and HALEY, D. E. Ricinus lipase, its nature and specificity. *Jour. Amer. Chem. Soc.* 57:2019-2021. 1935.
13. LOOMIS, W. E., and SHULL, C. A. Methods in plant physiology. McGraw-Hill Book Co., New York. 1937.
14. MILLER, E. C. A physiological study of the germination of *Helianthus annuus*. *Ann. Bot.* 24:693-726. 1910.
15. NIGHTINGALE, G. T.; SCHERMERHORN, L. G.; and ROBBINS, W. R. Some effects of potassium deficiency on the histological structure and nitrogenous and carbohydrate constituents of plants. *New Jersey Agr. Expt. Sta. Bull.* 499. 1930.
16. PETERS, E. Zur Keimungsgeschichte des Kürbissamens. *Landw. Vers. Sta.* 3:1-18. 1861.
17. RICHARDS, F. J. Physiological studies in plant nutrition. III. Further studies on the effect of potash deficiency on the rate of respiration in leaves of barley. *Ann. Bot.* 46:367-388. 1932.
18. ———. Physiological studies in plant nutrition. XI. The effect on growth of rubidium with low potassium supply and modification of this effect by other nutrients. Part I. The effect on dry weight. *Ann. Bot.* 5:249-261. 1941.
19. RICHARDS, F. J., and TEMPLEMAN, W. G. Physiological studies in plant nutrition. IV. Nitrogen metabolism in relation to nutrient deficiency and age in leaves of barley. *Ann. Bot.* 50:367-407. 1936.
20. SANDO, C. E. Lipides and their estimation in vegetable tissues. *Plant Physiol.* 3:155-184. 1928.
21. SCHIMPER, A. F. W. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. *Flora* 73:207-278. 1890.
22. SCHERBAKOV, A. P. On the quantity and distribution of certain enzymes in the organs and tissues of pea seedlings. *Biokhimiya* 10:68-78. 1945.
23. SNEDECOR, G. W. Statistical methods. 3d ed. Iowa State College Press, Ames, Iowa. 1940.
24. TIEDJENS, V. A., and WALL, M. E. The importance of potassium in the growth of vegetable plants. *Proc. Amer. Soc. Hort. Sci.* 36:740-743. 1938.
25. WALL, M. E. The role of potassium in plants. I. Effects of varying amounts of potassium on nitrogenous, carbohydrate, and mineral metabolism of tomato plants. *Soil Sci.* 47:143-161. 1938.
26. WATTS, V. M. Anatomical symptoms of nitrogen, phosphorus, and potassium deficiencies in seedling hypocotyls of tomato. *Arkansas Agr. Expt. Sta. Bull.* 366. 1938.
27. WINTON, A. L., and WINTON, KATE B. Structure and composition of foods. I. Cereals, starch, oil seeds, nuts, oils, forage plants. Wiley & Sons, New York. 1932.

